Letter

Leaf turgor loss point is correlated with drought tolerance and leaf carbon economics traits

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Leaf turgor loss point (π_{tlp}) indicates the capacity of a plant to maintain cell turgor pressure during dehydration, which has been proven to be strongly predictive of the plant response to drought. In this study, we compiled a data set of π_{tlp} for 1752 woody plant individuals belonging to 389 species from nine major woody biomes in China, along with reduced sample size of hydraulic and leaf carbon economics data. We aimed to investigate the variation of π_{tlp} across biomes varying in water availability. We also tested two hypotheses: (i) π_{tlp} predicts leaf hydraulic safety margins and (ii) it is correlated with leaf carbon economics traits. Our results showed that there was a positive relationship between π_{tlp} and aridity index: biomes from humid regions had less negative values than those from arid regions. This supports the idea that π_{tlp} may reflect drought tolerance at the scale of woody biomes. As expected, π_{tlp} was significantly positively correlated with leaf hydraulic safety margins that varied significantly across biomes, indicating that this trait may be useful in modelling changes of forest components in response to increasing drought. Moreover, π_{tlp} was correlated with a suite of coordinated hydraulic and economics traits; therefore, it can be used to predict the position of a given species along the 'fast–slow' whole-plant economics spectrum. This study expands our understanding of the biological significance of π_{tlp} not only in drought tolerance, but also in the plant economics spectrum.

Keywords: aridity index, carbon economics, drought tolerance, hydraulic safety margin, leaf turgor loss point.

Introduction

Leaf turgor loss point (π_{tlp}, MPa) indicates the capacity of a plant to maintain cell turgor pressure under drought stress. Traditionally, it is widely measured using the pressure–volume curve approach (Tyree and Hammel 1972, Lenz et al. 2006, Bartlett et al. 2012*a*); however, it can now be determined rapidly using a vapour pressure osmometer (Bartlett et al. 2012*b*, Marechaux et al. 2015). Plants with more negative π_{tlp} are able to resist leaf dehydration, thereby sustaining stomatal conductance, photosynthesis and growth under lower water availability (Tognetti et al. 2000, Baltzer et al. 2008,

Blackman et al. 2010). Previous studies have suggested that π_{tlp} may be strongly predictive of the drought response of a plant species (Bartlett et al. 2012*a*, Delzon 2015, Marechaux et al. 2015). For example, π_{tlp} has been reported as a good predictor of the capacity of a species for osmotic adjustment (Bartlett et al. 2014) and of the degree of isohydry vs anisohydry (i.e., the ability for stomatal control of plant water status; Meinzer et al. 2016). It is also related to other drought tolerance traits, including vulnerability to cavitation, and water potential at stomatal closure and at plant death (Bartlett et al. 2016).

The hydraulic safety margin is defined as the difference in water potential between the minimum value experienced in the field and the value at either 50% loss of leaf or stem xylem hydraulic conductivity. Since it indicates the hydraulic vulnerability of forests to drought (Choat et al. 2012) and predicts species mortality rates in plant communities that experience drought stress (Anderegg et al. 2016), it has become the subject of much research in the field of tree hydraulics (Delzon and Cochard 2014, Klein et al. 2014). Previous studies on hydraulic safety margin were mainly on the level of branches; however, fewer studies have been performed on hydraulic safety margin of leaves despite it being regarded as a hydraulic bottleneck and safety valve against hydraulic failure (Sack and Holbrook 2006, Pivovaroff et al. 2014). Moreover, the determination of hydraulic safety margin is time-consuming and difficult. Given the relationship between π_{tlp} and both minimum leaf water potential and vulnerability to cavitation, we expect π_{tlp} to serve as a convenient proxy of leaf hydraulic safety margin. To our knowledge, no previous studies have tested this hypothesis.

The concept of leaf economics spectrum (Wright et al. 2004) has now been extended to a single 'fast–slow' whole-plant economics spectrum for all plant organs and resources (Reich 2014). This hypothesis proposes that being fast or slow is a general feature of plants: species with the 'fast' strategy have high water transport capacity, low tissue density, short tissue life span, and high rates of resource acquisition and flux (Reich 2014). Indeed, strong relationships between hydraulic and carbon economy have been widely observed. For example, the correlations between hydraulic efficiency and photosynthetic capacity (Sack and Holbrook 2006, Fu et al. 2012, Zhu et al. 2013), or the trade-offs between cavitation resistance and carbon cost (Nardini et al. 2012, Jin et al. 2016). In addition,

several studies have examined the relationship between π_{tlp} and specific leaf area, a key functional trait (Bucci et al. 2004, Marechaux et al. 2015, 2016), but the results of these studies are in conflict with each other. Therefore, the relationship between π_{tlp} and leaf carbon economics traits needs extensive examination, in order to achieve a new insight into its role in the plant economics spectrum.

In this study, the π_{tlp} values of 1752 woody plant individuals belonging to 389 species representing nine major woody biomes in China were compiled from our own unpublished data and from the literature (Table 1 and see Table S1 available as Supplementary Data at *Tree Physiology* Online). Our first aim was to investigate the variations of π_{tlp} across biomes varying in water availability. Moreover, based on concomitant hydraulic and leaf carbon economics data when available in a same study (Table 1), our second aim was to explore the relationships between π_{tlp} and leaf hydraulic safety margins, and leaf economics traits. We hypothesized that π_{tlp} would predict leaf hydraulic safety margins and is correlated strongly with leaf carbon economics traits.

π_{tlp} is correlated with aridity index and leaf hydraulic safety margin

The linear mixed-effect models showed that aridity index, forest types and leaf habit were the three most significant factors that influenced the variance of π_{tlp} (Table S2 available as Supplementary Data at *Tree Physiology* Online). There was a positive relationship between π_{tlp} and aridity index (the ratio of mean annual precipitation to mean annual potential evapotranspiration) across species from the nine major biomes in China ($r = 0.42$, $P < 0.0001$), i.e., biomes from arid regions had a more negative π_{tlp} than those

Table 1. The nine leaf and branch traits used in this study. N, the number of species compiled for each trait.

Traits	Abbreviation	Unit	N	Definition
Leaf turgor loss point	π_{tlp}	MPa	389	Leaf water potential at which turgor pressure is zero, which is a determinant of the tolerance of leaves to drought stress
Minimum leaf water potential	ψ_{min}	MPa	167	The lowest midday leaf water potential experienced by a plant species during a year
Xylem water potential at 50% loss of hydraulic conductivity	$P50_{branch}$	MPa	188	An estimation of the vulnerability of xylem hydraulic conductivity to drought-induced cavitation
Leaf water potential at 50% loss of hydraulic conductance	$P50_{leaf}$	MPa	111	An estimation of the vulnerability of leaf hydraulic conductance to decreasing leaf water potential
Leaf hydraulic safety margin	SM_{leaf}	MPa	101	The difference between ψ_{min} and $P50_{leaf}$ ($\psi_{min} - P50_{leaf}$), which indicates potential risk of hydraulic failure in leaves
Specific leaf area	SLA	$cm^2\,g^{-1}$	301	Leaf area per dry mass, a key leaf functional trait that relates to plant performance such as growth and defense
Leaf density	LD	$g\,cm^{-3}$	88	Leaf dry mass per volume, which is one of the components of SLA and relates to photosynthesis and resistance
Maximum CO_2 assimilation rate	A_{max}	$nmol\,g^{-1}\,s^{-1}$	244	The maximum CO_2 assimilation capacity of leaves measured during the wet season under optimal conditions
Leaf life span	LLS	month	118	The time elapsed between leaf emergence and fall, which is considered as a balance between lifetime carbon gain and its cost

from humid regions (Figure 1). The variation of π_{tlp} across biomes in China is generally consistent with that observed in global meta-analyses (Bartlett et al. 2012a) and reinforces the conclusion that π_{tlp} may indicate drought tolerance at the scale of biomes (Bartlett et al. 2014, Marechaux et al. 2015, 2016). Additionally, we found
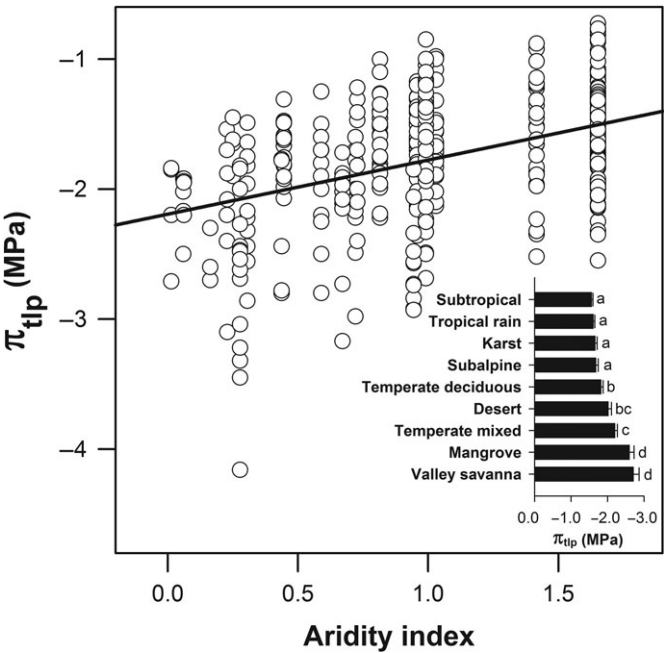

Figure 1. Relationship between leaf turgor loss point (π_{tlp}) and aridity index across woody plant species in China. Aridity index is calculated as the ratio of mean annual precipitation to mean annual potential evapo-transpiration (smaller values indicate more arid climate). Each point denotes one species in each site. Linear function: $y = -2.1930 + 0.4156x$, $R = 0.42$, $P < 0.0001$, $n = 428$ (39 species occurred in more than one biome). Inset: mean π_{tlp} of nine major biomes in China. Biomes (abbreviation): hot-dry valley savanna (valley savanna), mangrove forest (mangrove), temperate mixed broadleaved and coniferous forest (temperate mixed), desert shrubbery/woodland (desert), temperate deciduous broadleaved forest (temperate deciduous), subalpine mixed broadleaved and coniferous forest (subalpine), subtropical karst forest (karst), tropical rain forest (tropical rain) and subtropical evergreen broadleaved forest (subtropical). Error bars represent the standard error. Different letters indicate significant differences among forest types ($P < 0.05$; ANOVA).

significant positive correlations between π_{tlp} and minimum leaf water potential and vulnerability to cavitation in both branch xylem and leaves (Table 2). These results were consistent with other studies (Baltzer et al. 2008, Bartlett et al. 2016), reflecting a branch-to-leaf tissue coordination for drought tolerance.

Based on available data from three biomes, π_{tlp} was significantly and positively correlated with leaf hydraulic safety margins (SM_{leaf}) across species within each of the three biomes and within plant functional groups (evergreen and deciduous; Figure 2). This might be due to the fact that plants with higher leaf turgor loss point tends to exhibit isohydric behaviour (i.e., strong stomatal regulation of preventing hydraulic dysfunction; Meinzer et al. 2016), which indicates a smaller decline in leaf water potential during the drought period, thus leading to higher leaf hydraulic safety margin. The slope of the linear regression was significantly steeper for valley savanna than for the tropical and subtropical forests ($P < 0.01$, ANCOVA; Figure 2A); similarly, it was steeper for the evergreen species than for the deciduous broadleaved species ($P < 0.01$, ANCOVA; Figure 2B). These findings indicated that π_{tlp} can be used as a proxy of the degree of hydraulic vulnerability of leaves in response to drought, especially in species from arid environments and for evergreens.

We found that SM_{leaf} differed significantly among the three biomes and that subtropical evergreen broadleaved forest were composed of species with particular large safety margins (20 out of the 30 species showed values larger than 1 MPa; mean value was 1.70 MPa, with 95% confidence intervals ranging from 1.39 to 1.90 MPa; Figure 2). Li et al. (2015) also reported a wide hydraulic safety margin of branches in the same forest (mean value was 1.67 MPa). These results are contrary to a recent global analysis showing that angiosperm species from different biomes all operate within a narrow range (<1 MPa) of branch hydraulic safety margins regardless of their rainfall environment (Choat et al. 2012). It also contradicts current opinion that the hydraulic safety margin of leaves is much narrower than that of branches (Bucci et al. 2013) despite branches being more resistant to cavitation and operating at a higher (less negative) water potential than terminal leaves (Scholz et al. 2014, Nolf et al. 2015). This might be due to the subtropical moist

Table 2. Pearson's correlation coefficients between each pair of traits. Trait abbreviations are shown in Table 1. Significant correlations ($P < 0.05$) are bold and underlined.

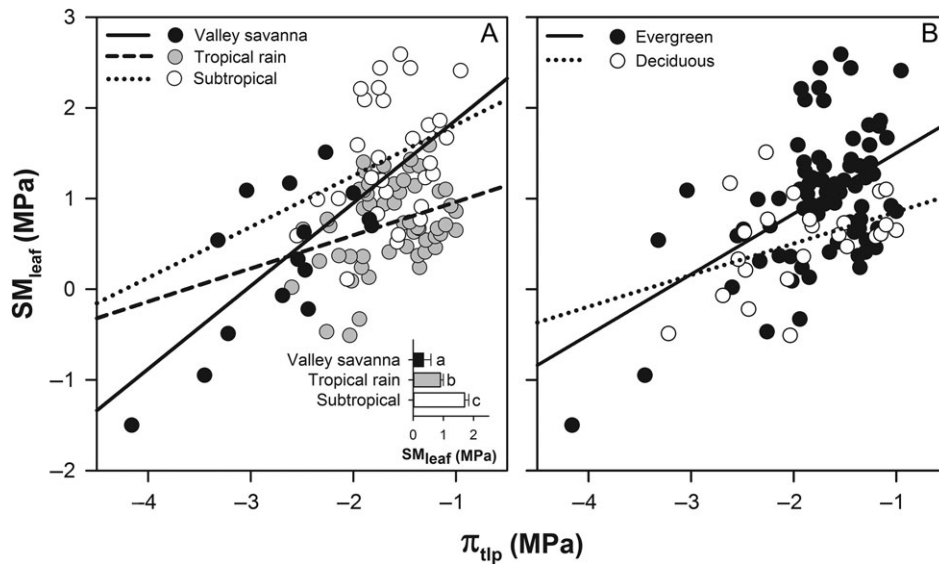| Traits	π_{tlp}	ψ_{min}	$P50_{leaf}$	SM_{leaf}	$P50_{branch}$	SLA	LD	LLS	A_{max}
π_{tlp}									
ψ_{min}	**0.78**								
$P50_{leaf}$	**0.45**	**0.63**							
SM_{leaf}	**0.50**	**0.53**	**−0.32**						
$P50_{branch}$	**0.44**	**0.40**	**0.51**	0.11					
SLA	**0.36**	**0.33**	0.17	0.09	0.19				
LD	**−0.38**	**−0.58**	**−0.54**	−0.38	−0.36	**−0.34**			
LLS	**−0.60**	**−0.56**	**−0.47**	−0.24	**−0.47**	**0.47**	**0.64**		
A_{max}	**0.27**	0.13	**0.32**	−0.13	**0.27**	**0.62**	−0.27	**−0.46**	

Figure 2. Relationship between leaf turgor loss point (π_{tlp}) and leaf hydraulic safety margin (SM_{leaf}). Note that only SM_{leaf} data from hot-dry valley savanna (valley savanna, dark grey), tropical seasonal rain forest (tropical rain, grey) and subtropical evergreen broadleaved forest (subtropical, white) are available. Linear functions in (A): valley savanna, $y = 2.7816 + 0.9152x$, $r = 0.50$, $P < 0.01$, $n = 15$; tropical rain, $y = 1.3308 + 0.3670x$, $r = 0.32$, $P < 0.05$, $n = 56$; subtropical, $y = 2.3763 + 0.5625x$, $r = 0.32$, $P = 0.07$, $n = 30$. Linear functions in (B): evergreen, $y = 2.1705 + 0.6687x$, $r = 0.51$, $P < 0.001$, $n = 77$; deciduous, $y = 1.2038 + 0.3492x$, $r = 0.35$, $P < 0.05$, $n = 24$. Inset: mean SM_{leaf} of the three forest types. Error bars represent the standard errors. Different letters indicate significant differences among biomes ($P < 0.05$; ANOVA).

monsoon climate of the present study, which has abundant rainfall and no severe drought events, so that it does not exert a strong selective pressure to enhance hydraulic segmentation between leaves and branches (Villagra et al. 2013, Zhu et al. 2016).

The hot-dry valley savanna with the lowest leaf turgor loss point showed the smallest hydraulic safety margin among the three biomes (Figure 2), which is possibly an adaptive trait of the savanna species growing in arid climate. This 'risky' strategy would allow stomatal opening to maximize carbon gain when the drought is mild, so that these species can shed leaves when the water deficit is severe at the peak of the dry season. However, this finding (i.e., small leaf hydraulic safety margin in hot-dry valley savanna from arid climate) contradicts somewhat a recent study showing wider branch hydraulic safety margins (calculated as the difference in water potential between the value of water potential at stomatal closure and at that at 12% loss of branch hydraulic conductivity) with increasing cavitation resistance (Martin-StPaul et al. 2017). One explanation is that hydraulic safety margins at the level of branches and leaves may have inconsistent trends; for example, Bucci et al. (2013) found that as soil water potential decreased, leaf hydraulic safety margin decreased significantly, though branch hydraulic safety margin remained high and constant across Patagonian shrub species. In addition, Johnson et al. (2016) revealed that species with smaller leaf hydraulic safety margin tended to have stronger vulnerability segmentation (larger differences in P50 between branch and leaf), which represented an alternative strategy (compared with strict stomatal regulation) that leaves act as a hydraulic 'safety valve' to maintain hydraulic

functioning of branches (Bucci et al. 2012, Nolf et al. 2015). Measuring single hydraulic properties on single plant organ may not accurately evaluate the overall hydraulic strategy at the level of whole plant (Meinzer et al. 2010, Johnson et al. 2016). We therefore recommend focusing on multiple hydraulic mechanisms and organs (e.g., leaf, branch and root) for an accurate assessment of the degree of drought risks.

π_{tlp} predicts the position of a species along the 'fast–slow' plant economics spectrum

The results of Pearson correlation showed that π_{tlp} was positively correlated with specific leaf area (SLA) and maximum CO_2 assimilation rates (A_{max}), and was negatively correlated with leaf life span (LLS) and leaf density (LD; Table 2). Plant species with more negative π_{tlp} tended to have higher LD and lower SLA, which confirms that increased leaf turgor maintenance is associated with increased leaf carbon investment (Villagra et al. 2013). A significant π_{tlp}–A_{max} relationship was also found in 10 temperate tree species (Jin et al. 2016); however, the path analysis indicated that this relationship might be driven by an indirect impact of coordination between π_{tlp} and SLA, rather than a direct impact of π_{tlp} on A_{max} (Figure 3). Given that lower (more negative) π_{tlp} related to lower carbon gain and higher leaf construction costs (i.e., a longer time to amortize carbon investments), it is no wonder that there was a significant negative correlation between π_{tlp} and LLS, which has also been shown in 12 tree species in a natural tropical dry forest (Fu et al. 2012).
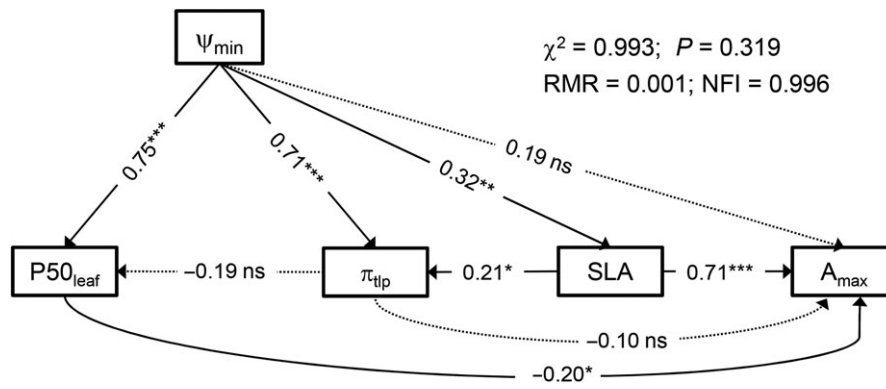
Figure 3. Path model analysis of the relationships linking minimum leaf water potential (ψ_{min}), leaf water potential at 50% loss of hydraulic conductance (P50$_{leaf}$), leaf turgor loss point (π_{tlp}), specific leaf area (SLA) and maximum CO_2 assimilation rate (A_{max}). Note that the only five traits of 111 species are used for this analysis because there are too many missing values for other traits. Arrows indicate the proposed links between variables. Dotted lines indicate non-significant paths. Path coefficients are shown on the arrows (ns, $P > 0.05$; *, $P < 0.05$, ***, $P < 0.001$). Overall fit statistics for path model (χ^2, Chi-square; RMR, root mean square residual; NFI, normed fit index) are shown at the up right corner of the figure.

Our results also demonstrated close relationships between cavitation resistance and leaf carbon economics traits; for example, there was a significant relationship between A_{max} and P50 (i.e., P50$_{leaf}$ and P50$_{branch}$; Table 2). In turn, according to path analysis results, P50$_{leaf}$ had a direct influence on A_{max} (Figure 3). Similarly, Maherali et al. (2006) also found a strong relationship between vulnerability to cavitation (in branches and roots) and leaf gas exchange rates in 14 co-occurring temperate tree species. Overall, our study supports that there is a functional link between different physiological strategies associated with species performance (i.e., hydraulic function, osmotic properties and carbon economics) and between leaf and stem (Tognetti et al. 2001, 2002, Westoby and Wright 2006, Nardini et al. 2012), thus supporting the single 'fast–slow' plant economics spectrum hypothesis (Reich 2014). We suggest that π_{tlp} may play a central role in generating this spectrum because it is correlated with a suite of coordinated hydraulic and carbon economics traits.

Conclusion

This study expands our understanding of the biological significance of π_{tlp}, not only in drought tolerance but also in the plant economics spectrum more generally. Our study demonstrates that π_{tlp} is a strong predictor of leaf hydraulic safety margins, suggesting that π_{tlp} can be used in modelling changes in forest community composition in response to increasing drought stress. Moreover, we find that π_{tlp} was closely correlated with both hydraulic and economics traits, and could be extended to predict the position of a species along the 'fast–slow' plant economics spectrum.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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